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Prospects for biological control of rodent populations *

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Pathogens and predatory animals are the main agents used for the biological control of rodents. The pathogens that have been used are of the genus Salmonella; *none is rodent-specific and all can cause severe infection in man and domestic animals. Furthermore, rodents frequently develop immunity to, and become carriers of, these organisms, and there is little to commend their use, except in lightly populated areas where control is infrequently applied. The relationships of five predator species with their rodent prey have been examined. The monitor lizard, mongoose, and ferret were for different reasons found to be unsatisfactory, and there is not yet sufficient evidence to warrant further releases of the Japanese weasel. Domestic and feral cats control rodents well in some situations but only after some other agent has removed a large part of the rodent population.*

Biological control may be defined in different ways. Howard (1967), for instance, in discussing biological control of vertebrate pests, defines it as " an attempt to reduce the population density of a pest species... either by increasing predation, manipulating the conditions of the habitat, introducing or stimulating epizootics, or by the application of antifertility agents." Entomologists have been much concerned with biological control and can claim to have achieved some spectacular results with insects. Their definition of biological control is much more restricted. Another view is that biological control is a part of the natural control of animal populations, the action of parasites, predators or pathogens on a host or prey population producing a lower general equilibrium position than would prevail in the absence of those agents. For the entomologist the alternative to biological control is chemical control; integrated control is a form of pest control that combines both. The writer is inclined to accept the second definition because it is simpler and more in agreement with the prevailing terminology. Consequently, since there are no known parasites that could control rodent populations, this review is restricted to agents—pathogens (i.e., bacteria and viruses) and predators.

* This paper was written in 1970 and does not take account of papers published since that date.

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CONTROL BY PATHOGENS

The pathogens used to control noxious animals comprise different bacteria (often referred to as " rat viruses ") and one virus, the myxomavirus (Fenner & Ratcliffe, 1965). The latter is the only pathogen that is known to be specific to one species (wild and domestic rabbits, *Oryctolagus cuniculus*); even closely related species (such as the European hare, *Lepus europaeus*) are not affected by it. According to Elton (1942), who reviewed the origins, development, and results of rodent control measures using pathogens, Pasteur was the first to suggest the use of microorganisms to infect a harmful species without attacking other species.

In rodent-control operations in Europe, pathogens were first used against voles (*Microtus* spp.), the most important rodent species with respect to crop damage, particularly during the well-known cyclic outbreaks. In Germany, Loeffler (1892) developed a mouse-typhoid culture (later known as *Salmonella typhimurium*) that he used against a plague of voles ravaging wheat fields in Thessaly. Danysz (1893, 1900, 1913) examined voles found dying during an epidemic in France in 1893 and cultured a microorganism (later named *Salmonella enteritidis* var. *danysz*) that killed rats in the laboratory. Danysz (1893) used this microorganism first against voles and later against commensal rats (*Rattus rattus* and *R. norvegicus*).

In Denmark, after studying a large number of bacteria, Bahr (1905, 1931, 1938, 1947) developed a pathogen he called " Ratin " (later identified as *S. enteritidis*), which, according to a limited number of experiments, was deadly to rats but not to man and other animals. In his later work Bahr advocated that Ratin treatment be followed up by the use of " Ratinin ", a preparation containing the well-known rat poison red squill—an early form of integrated control. Issatschenko (1898) developed a culture from an epidemic among wild brown rats (*R. norvegicus*) in St. Petersburg and Mereshkowsky (1895) obtained cultures from an epidemic of marmots (*Citellus* spp.) in Samara.

Since the early 1900s the use of pathogens in rodent control has spread widely, particularly in Europe. In France, the Institut Pasteur in Paris produced and sold the " virus Pasteur " and " virus Danysz " until about 1958 (Giban & Grolleau, 1967). Pathogenic bacteria were used in Poland for the first time in 1926 by Trawinski (1931), the aim being to control massive populations of field mice by broth cultures of *S. typhimurium* (Brodniewicz, 1959, and unpublished data). At about the same time " Ratin " and " Ratinin " were also used and an 80–92% mortality of field rodents was reported. As a result of representations by epidemiologists and hygienists, however, the use of pathogens was later greatly restricted, although the appearance of large numbers of rodents in 1945–47 led to another period of massive use of *S. enteritidis* var. *danysz* that lasted until 1950; according to Brodniewicz (unpublished data) it was very successful. Bacteriological control of rodents has not been practised in Poland since 1950, although the method has not been prohibited. The use of bacterial poisons was prohibited in Germany in 1934 (*Tierärztl. Mitt.*, 1934).

In the USSR, the rodent problems are of considerable magnitude, and pathogens have been widely used for control since the discoveries of Issatschenko (1898) and Mereshkowsky (1895). The advantages of control by pathogens over chemical control (low cost, disastrous epizootics among small rodents, and safety) prevailed over the reservations of the hygienists. In recent years about 150 laboratories in the USSR have produced 350 tons of bacterial preparations. Four strains of *Salmonella* are being used at present: the Issatschenko culture, strain no. 5170, the Mereshkowsky strain, and strain BK2C. Mortalities of 65–100% among the smaller rodents and 30–80% in *R. norvegicus* have been claimed (Gromova, 1962).

Since the use of pathogenic bacteria for rodent control became established in Western Europe, research workers have been puzzled by the variability of the results (see Elton, 1942). Danysz had complete success in 50% of his trials, partial success in 30% and failure in 20%. Abel (1901) reported 100% mortality in laboratory experiments in which wild and white *R. norvegicus* were fed with *B. danysz*. However, in five field trials the results were different: in one trial only two dead rats were found although the remainder disappeared; in two other experiments there was a marked decrease of the number of rats while in two further trials nothing was achieved.

The belief that the pathogens were species-specific did not hold for long. Handson et al. (1908) were among the first to describe an epidemic of enteritis in Britain that was traced to a " Liverpool virus " laid for rats. Spray (1926) reported an epidemic of 135 cases of acute gastroenteritis in a student hostel. The organisms isolated from the affected students were identical with those of the " rat virus " in the commercial bait laid shortly before. However, it was only in the early 1940s that adequate information on the principal cultures used in rat and mouse control in Great Britain became available in two reports from the University of Oxford Bureau of Animal Population, and in that of Leslie (1942). Of six " viruses " used at that time in Britain four (the Liverpool and Danysz varieties, " Ready Rat Relief ", and " Ratin ") were assigned to the *S. enteritidis* var. *danysz* group, and two (London and Institut Pasteur) could not be distinguished from the classical *S. enteritidis* group. Both these groups were found not to be specific to rodents but to be pathogenic to man and to domestic animals.

Since that time evidence has accumulated concerning the links between rat pathogens and infection of other animal species by *Salmonella* (Dathan et al., 1947; Clarenburg et al., 1958). Taylor & Atkinson (1955) provided further evidence of infections with *S. enteritidis*, from bacterial rodenticides of both the *Jena* and *Danysz* varieties, in man and animals. Between 1944 and June 1955, *S. enteritidis* var. *jena* accounted for 1 267 known cases (21 fatal) and *S. enteritidis* var. *danysz* for 413 cases (2 fatal) in Britain. A number of animals were also found to be infected by both varieties. Collins et al. (1966) found that *S. enteritidis* was highly virulent to mice but that survivors were completely resistant to reinfection and eliminated a large challenge dose of the virulent organism within 72 hours. Also several workers reported a significant increase in the incidence of *Salmonella* infections in man and animals in the Netherlands (Bergsma, 1959) and in the USA (Dack, 1963), where 650 types of *Salmonella* were identified, all of which may cause gastroenteritis in man.

Further studies revealed that individual rats and other animals may carry *Salmonella* without harmful effects. Ludlam (1954) isolated infections in 4.4% of 518 rats from the Nottingham area in England. Nearly half of a sample of rats from the Kielce area, Poland, were carriers of *Salmonella* strains, including *S. enteritidis* and *S. typhimurium* (Cwiakata & Chmielewska, 1952). Massive fatal epizootics among gulls were caused by *Bacterium enteritidis breslau* (Schmidt, 1954) and among seagulls, mallards, and London pigeons (Farrant et al., 1964) by *S. typhimurium*; under favourable conditions these strains were capable of infecting man. Frank (1953), studying the collapse of plagues of field rodents in the Federal Republic of Germany, considered that the rapid termination of such plagues was probably due to the exhaustion of an internal physiological mechanism and not to epidemics. Swain (1961) discussed the role of wildlife in the epidemiology of certain human diseases and concluded as follows: " The folly of the deliberate introduction of certain bizarre types of Salmonellae as ' poisons ' into rodent populations has been demonstrated on countless occasions when epidemics of gastroenteritis in man due to the selfsame organism have resulted." Finally, it would appear that the evidence against the use of *Salmonella* briefly reported above must have had a bearing on the following conclusion of the Joint FAO/WHO Expert Committee on Zoonoses (1967): " In connexion with salmonellosis in rodents it should be reemphasized that salmonellas should under no circumstances be used as rodenticides. Rodents rapidly develop resistance to *Salmonella* serotypes; thus, this method has little practical value. Moreover, it has been shown in different countries that such practices are a public health hazard because the serotypes used are also dangerous to man."

CONTROL BY PREDATORS

The concept that predators, both native and introduced, are an effective and important agent for controlling undesirable animal populations is almost as old as agriculture. According to Zeuner (1963) " since rodents became storage pests as soon as the problem of preserving a supply of grain from harvest to harvest was solved " some small carnivores —such as the cat, the ferret, and the mongoose— " inevitably became the associates of man, both having the same goal." In Egypt the cat appeared as a domestic wild animal in the New Kingdom (sixteenth century B.C. onwards).

Elton (1942) provides a succinct and vivid account of the role of predators in relation to rodents in Europe and other continents up to about 1940. The observations recorded on the predator–prey relationship in connexion with the cyclic plagues of field rodents are of particular interest.

The predatory animals that have been used to control rodent populations are listed in order of increasing importance as follows: the ferret (*Putorius putorius*), the monitor lizard (*Varanus indicus*), the mongoose (*Herpestes auropunctatus*), weasels (mainly *Mustela sibirica itatsi*), and domestic and feral cats (*Felis catus*).

Ferrets have been liberated in New Zealand to control the wild rabbit, *Oryctolagus cuniculus* (Wodzicki, 1950), but are rarely used to control rats (*Scient. Amer.*, 1944).

Monitors were introduced by the Japanese into some of the western Caroline Islands (e.g., the Ifaluk atoll) and Laird (1963) suggested that *V. indicus* merited further study as a possible candidate for introduction into the Tokelau Islands to reduce the number of rodents and hence the severe damage they cause to coconuts. Uchida (1966) surveyed the effect of monitor lizards on rat populations on Ifaluk atoll and concluded that monitors did not control rats as well as had been expected.

The small Indian mongoose (*Herpestes auropunctatus*) was originally introduced into Jamaica and other islands of the Caribbean about 1870 as a predator on rodents. In 1883 the mongoose was introduced into Hawaii and at a later stage into Fiji (Tomich, 1969). In Puerto Rico, where the mongoose was introduced from Jamaica for rodent control, Pimentel (1955) found that during the first 10–15 years all reports were favourable as the mongoose had a marked initial effect on the rodent population. The omnivorous habits of the mongoose were confirmed but rat remains were found only in 2.5% of stomach contents. On the other hand the number of destructive and dangerous arthropods eaten by the mongoose was of slight economic significance. However, this advantage was outweighed by the fact that the mongooses in Puerto Rico are an important reservoir and vector of rabies. In Trinidad, Williams (according to Tomich, 1969) concluded that, except in a few ecological settings, the mongoose is undesirable. Finally, in the Virgin Islands, Seaman (1952) and Seaman & Randall (1962) confirmed that mongoose food was extremely diverse, including insects, reptiles, birds, and rodents. They also reported predation on deer fawns and the disappearance or drastic reduction of iguanas, ground lizards, and two kinds of native snake.

No information is available on the food or the status of the mongoose in Fiji but there is some basic information on its food and feeding habits in the Hawaiian islands. The mongoose was liberated on Hawaii, Maui, and Oahu in 1883 but not on Kauai. Since its liberation this species has been the subject of a number of studies (Pearson & Baldwin, 1953; Kami, 1964; Hinton & Dunn, 1967) recently summarized by Tomich (1969). Again, as in the West Indies, there were enthusiastic reports of the rat-killing capacity of the mongoose during the first decade after liberation. These reports were followed by accounts of intense predation on bird species such as the ring-necked pheasant (*Phasianus colchicus*). Other authors (Elder, 1958; Walker, 1966) consider the mongoose to be a factor in the decline of the nene or Hawaiian goose (*Branta sandvicensis*); and King & Gould (1961) hold it to be largely responsible for the extermination of the Manx shearwater (*Puffinus puffinus*) in the Hawaiian islands. Tomich (1969), summing up the results of the work of Pemberton (1933), Baldwin et al. (1952), and Kami (1964), reports a " high incidence of rodent remains in mongoose excreta from sugar-cane fields ... and nothing to suggest that highly beneficial insects were taken." While the above-mentioned research workers agree that canefield mongooses feed largely on rodents, Tomich (1969) doubts " that they may act as a prominent factor in rodent control ... Rodents are still a major source of economic loss to cane planters locally on all islands. Problems on Oahu, Maui and Hawaii are perhaps as great or greater than on Kaui where the mongoose does not exist, but actual comparative studies are lacking."

Weasels and other representatives of the Mustelid family are important rodent predators. Elton (1942) records that stoats and weasels were among the predators that "were unusually numerous upon the scene of the outbreak " of vole plagues in Scotland and in northern Canada. Three Mustelid species (the ferret, *Putorius putorius*; the stoat, *Mustela erminea*; and the weasel, *Mustela nivalis*) were introduced into New Zealand for rabbit control (Wodzicki, 1950) but, particularly the stoat and the weasel, eat rodents as a large part of their diet.

Japan has shown a considerable interest in weasels as biological agents for rodent control. Weasels have been introduced to some offshore islands of Hokkaido and Kyushu and more recently a massive liberation of Japanese weasels (*Mustela sibirica itatsi*, Temminck & Schlegel) was carried out in several islands of the Ryukyu Archipelago (Uchida, 1968 and unpublished data). As in other sugarcane producing countries—e.g., the Hawaiian islands or Queensland, Australia—roof rats *(Rattus rattus)* had been responsible for severe damage to crops. Between March 1967 and January 1968 a total of 6 843 weasels were liberated on 17 islands with a total area of 97 754 ha, i.e., about 7 weasels per 100 ha at a total cost of $136 869 or $20 a head. In addition to the liberation of weasels, acute and anticoagulant rodenticides were also used during that period. It is, therefore, difficult to separate the effects of weasel predation from those of the poisons. Furthermore, more weasels were liberated during Uchida's (1969) surveys so that ecological equilibrium between weasels and rats has not been and will not be reached for a few years. The animal remains that could be identified in 32 samples of weasel excreta, most of which were collected in February and March, were: rat in 9 samples, bird in 6, frogs and toads in 7, and insects in 19. It is difficult to draw any definite conclusions from such small samples but the figures do show the great diversity of the weasels' food in the Ryukyus, and also the effect that weasels are likely to have on the native fauna of these islands.

The findings of Uchida are reported at some length because Uchida (unpublished report), following Laird (1963 and unpublished report), concluded that " further consideration of the possibility of experimental introduction of the Japanese weasel [*Mustela sibirica itatsi*, Temminck and Schlegel] into tropical Pacific Islands would be very pertinent."

The writer, after careful examination of the results of Uchida's study, considers that the evidence is not sufficient to warrant such action in the Tokelau Islands or any other low island in the Pacific where the environment is extremely vulnerable. Moreover, judging by the latest unpublished evidence supplied by Uchida on the status of the weasels in the Ryukyus, it is too early to decide whether the introduction of weasels there will be beneficial in the long run.

Cats are the oldest carnivores employed by man in the biological control of rodents and there are more observations on the preying habits of cats than on those of other carnivores.

Buchanan (1908, 1910) reported the absence of plague in villages in India that had many cats; and Loir (1927, 1932, 1933, 1935) considered that rodent problems in dock areas could be solved by cats specially bred for a high rat-killing ability. However, it was Elton (1953) who carried out the first scientific investigation to compare the efficiency of cats and human beings in rat control. On five farms in England, the rats were poisoned and then cats were introduced and a fifth had no cats after the poisoning. The four farms with cats remained almost free from rats while the fifth farm suffered recurrent rat infestation. The author concluded that cats will maintain the immediate area of farm buildings rat-free if they are introduced in sufficient numbers after poisoning and if a part of their food is supplied as milk.

Interesting information on the status of cats as predators of wildlife in Hawaii was supplied by Tomich (1969), and Hubbs (1951) provided similar information for California. Feral cats in the Sacramento Valley, California, have a diet that changes with the season and consists mostly of rodents but also includes significant numbers of ducks, pheasants, song birds, and rabbits. Among the cat stomachs examined about 22% included the remains of a pheasant or a duck.

Pearson (1964, 1966) has studied the role of predatores during a field-mouse cycle. The population of rodents was estimated to assess the standing crop of the four rodents in the area. An analysis of carnivores' droppings collected systematically in the area at the time when the rodent population reached a peak, and afterwards, gave the number and proportion of each rodent eaten by carnivores (feral cats, grey foxes, racoons, and skunks) before the next spring. Two conclusions that are of particular relevance to the present paper emerge from Pearson's studies. First, the selectivity of the predators: *Microtus* was the preferred prey (88% of the population was eaten) followed by *Reithrodentomys* (33%) and *Mus* (7%). When the first two rodents became scarce, the carnivores turned to gophers (*Thomomys*) and finally to wood rats (*Neotoma*). The second important conclusion from Pearson's work was that carnivore–prey interaction is an important if not essential part of the microtine cycle. Carnivores do not destroy a mouse cycle when it is at its peak, but reduce the cycle down to a very low level after something else has helped to remove the peak mouse population. Carnivores can then keep the numbers at a low level for an appreciable period. According to Pearson small numbers of carnivores would be effective and the length of the delay in recovery would depend upon how long suitable alternative food could support enough carnivores to control the few surviving preferred prey.

CONCLUSIONS

The use of pathogens in rodent control has many drawbacks. Although some workers have claimed spectacular results, particularly in breaking cyclic plagues of rodents, it is now well established that rodents quickly develop immunity, allowing a speedy recovery of the population. Recent bacteriological research has shown that practically all " rat viruses " are in fact virulent *Salmonella* species dangerous to man and domestic animals. A large number of cases of food poisoning, some fatal, during the last few decades have been traced to pathogens contained in rodent baits.

Emergency situations, such as those that prevailed in Poland in 1945–47, are exceptions for which the use of pathogens may be justified. The devastation of the country by war was combined with a cyclic outbreak of field rodents that threatened an extremely serious loss of agricultural products. The vast territories of the USSR and of some central Asian countries may be another exception: the sparse population and the infrequent application of the pathogens render human infection less likely. However, it would be useful to know the comparative effectiveness of bacterial control methods and conventional methods, such as the use of anticoagulants following that of acute poisons.

Students of predation do not agree on the value of different carnivores as agents for the control of rodents. Howard's (1967) statement that " vertebrate predators usually do more to increase population densities of field rodents than they do to depress them " implies that " without predation, self-limitation stress factors come into play at lower density levels, and that these forces operate as population controls more drastically than does predation." Errington (1946, 1956), concluding a life-long study of predation on rodents and birds, considered predation as one of several factors, but not necessarily the most important, affecting the size of animal populations. Similarly, Pearson (1966) demonstrated that carnivores are an intrinsic part of rodent cycles and that they can modify these cycles but are unable to prevent them. Finally, Uchida and Laird both believe that integrated rodent control could be achieved on Pacific islands by predators.

The evidence collected by the writer, in general, supports the views of Errington and Pearson that predators cannot effectively control rodent populations. Furthermore, the liberation of exotic predators in vulnerable environments, such as in the

Pacific islands, can have serious ecological consequences. The examples of the introduction of the mongoose in the Hawaiian islands and of mustelids in New Zealand should serve as a warning. The biological control of rodents appears to be ineffective in some environments and may even be dangerous in others. Alternative methods such as the judicious use of poisons, especially anticoagulants, and habitat modification should be tested first. Work in the Pacific by the author (1968a, 1968b, 1969a, 1969b, 1970) has shown that these methods have been successful in the vulnerable environments of the atolls.

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RÉSUMÉ

PERSPECTIVES DE LA LUTTE BIOLOGIQUE CONTRE LES POPULATIONS DE RONGEURS

On peut définir la lutte biologique comme l'action de parasites, d'agents pathogènes ou de prédateurs sur une population hôte (ou proie) qui a pour résultat d'amener cette population à un niveau d'équilibre inférieur à celui qui existerait en leur absence. Les moyens de lutte biologique contre les rongeurs sont représentés par des agents pathogènes (bactéries et virus) et des prédateurs, autochtones ou importés.

Dès les années 1890, on a entrepris d'utiliser divers agents pathogènes pour détruire les rongeurs. La plupart d'entre eux étaient des micro-organismes isolés lors d'épidémies frappant les petits rongeurs sauvages en Europe, en Amérique et en Asie. Décrits sous différents noms, souvent appelés « virus du rat » et identifiés ultérieurement comme des souches de *Salmonella typhimurium* et *S. enteritidis*, ils ont été considérés, sur la base de quelques essais, comme mortels pour les rongeurs et inoffensifs pour les autres animaux et pour l'homme. Aussi leur emploi s'est-il généralisé. Mais la fréquence des échecs, la survenue de cas d'infection grave chez l'homme et les animaux domestiques et l'apparition d'une résistance chez les rongeurs ont conduit à les abandonner. Cependant les *Salmonella* sont encore utilisées en URSS, apparemment avec succès, mais leur emploi est limité à des régions très peu peuplées où le risque de contamination humaine accidentelle est quasi inexistant.

Divers prédateurs ont été récemment utilisés dans la lutte biologique contre les populations de rongeurs: le furet (*Putorius putorius*), le varan (*Varanus indicus*), la mangouste (*Herpestes auropunctatus*), la belette (*Mustela sibirica itatsi*), le chat domestique et le chat sauvage (*Felis catus*). Les trois premiers n'ont pas fait preuve de l'efficacité escomptée et certains ont eu une influence néfaste sur le plan écologique. Il est encore trop tôt pour évaluer l'intérêt de la belette japonaise en tant qu'agent de destruction des rongeurs, mais il est probable que l'introduction de cette espèce dans des îles entraînera de profondes perturbations de la faune locale. Le chat est un prédateur efficace, capable de maintenir à un faible niveau une population de rongeurs si celle-ci a été au préalable fortement réduite par d'autres moyens.

L'auteur conclut que les prédateurs, disponibles sur place ou importés, ne peuvent intervenir dans la lutte biologique contre les rongeurs que si la population à détruire a déjà été en grande partie éliminée par d'autres agents létaux. Il suggère qu'avant d'introduire un prédateur, notamment dans les écosystèmes insulaires, on procède d'abord à des essais judicieux de rodenticides, anticoagulants ou autres, ou de modification de l'habitat.

REFERENCES

Abel, R. (1901) *Dtsch. med. Wschr.*, **27**, 869-870

Bahr, L. (1905) *Zbl. Bakt., I. Abt. Orig.*, **39**, 263-274

Bahr, L. (1931) *La destruction des rats et le système "Ratin"*. In: *Première Conf. intern. du Rat, Paris, 1928*, pp. 248-255

Bahr, L. (1938) *Z. Infekt.-Kr. Haustiere*, **54**, 44-56

Bahr, L. (1947) *Maanedsskr. Dyrlaeg.*, **59**, 161-192

Baldwin, P. H. et al. (1952) *J. Mammal.*, **33**, 335-356

Bergsma, C. (1959) *T. Diergeneesk.*, **84**, 872-891

Brodniewicz, A. (1959) *Deratyzacja w Polsce [Rat eradication in Poland]*. In: *Polsko-Czechoslowackie Sympozjum DDD, Warsaw, 9-11 December, 1957. Biuletyn DD i D*, **3**, No. 1

Buchanan, A. (1908) *Brit. med. J.*, **1**, 1285-1286

Buchanan, A. (1910) *Brit. med. J.*, **2**, 305-307

Clarenburg, A. et al. (1958) *Ned. T. Geneesk*, **102**, 2095-2097. *Bull. Hyg. (Lond.)*, 1959, **34**, 653

Collins, F. M. et al., (1966) *J. exp. Med.*, **124**, 601-619

Cwiakata, A. & Chmielewska, M. (1962) *Med. dośw. Mikrobiol.*, **4**, 135-146

Dack, D. M. (1963) *Salmonella food infections*. In: Hull, T. C., ed., *Diseases transmitted from animals to man*, 5th ed., Springfield, Ill., C. C. Thomas, pp. 210-234

Danysz, J. (1893) *J. Agric. prat., Paris*, **57**, 920-921

Danysz, J. (1900) *Ann. Inst. Pasteur*, **14**, 193-201

Danysz, J. (1913) *Les campagnols : histoire naturelle, invasions, maladies contagieuses: préparation en grand des cultures des microbes pathogènes : organisation d'une distribution systématique*, Paris, Institut Pasteur

Dathan, J. G. et al. (1947) *Lancet*, **252**, 711

Elton, C. S. (1942) *Voles, mice and lemmings*, Oxford, Clarendon Press

Elder, W. H. (1958) *Ninth Annual Report of the Wildfowl Trust*, Honolulu, Hawaii, pp. 112-117

Elton, C. S., (1953) *Brit. J. Anim. Behav.*, **1**, 151-155

Errington, P. L. (1946) *Quart. Rev. Biol.*, **21**, 144-177, 221-245

Errington, P. L. (1956) *Science*, **124**, 304-307

Farrant, W. M. et al. (1964) *Mth. Bull. Minist. Hlth Lab. Serv.*, **23**, 231-232

Fenner, F. & Ratcliffe, F. N. (1965) *Myxomatosis*, London, Cambridge University Press

Frank, F. (1953) *Nachr. Bl. dt. PflSchutzdienst, Berl.*, **5**, 165-166

Giban, J. & Grolleau, G. (1967) *Phytoma*, No. 191, pp. 29-30

Gromova, M. I. (1962) *Referat. Žur., biol.*, **81**, 235

Handson, L. et al. (1908) *Brit. med. J.*, **2**, 1547-1550

Hinton, H. E. & Dunn, A. M. S. (1967) *Mongooses: their natural history and behaviour*, Davis, Calif., University of California Press

Howard, W. E. (1967) *Biological control of vertebrate pests*. In: *Proc. Third Vertebrate Pest Conf.*, Davis, Calif., University of California Press

Hubbs, E. L. (1951) *Calif. Fish Game*, **37**, 177-189

Issatschenko, B. (1898) *Zbl. Bakt.*, **23**, 873-874

Joint FAO/WHO Expert Committee on Zoonoses (1967) *Wld Hlth Org. techn. Rep. Ser.*, No. 378

Kami, H. T. (1964) *Zoonoses Res.*, **3**, 165-170

King, W. B. & Gould, P. J. (1961) *Living bird*, **6**, 163-186

Laird, M. (1963) *Rats, coconuts, mosquitoes and filariasis*. In: *Proc. 10th Pacific Sci. Congress*, Bishop Museum Press, 535-542

Leslie, P. H. (1942) *J. Hyg. (Lond.)*, **42**, 552-562

Loeffler, E. (1892) *Zbl. Bakt.*, **12**, 1-17

Loir, A. (1927) *Rec. Méd. vét.*, **103**, 894-896

Loir, A. (1932) *Rev. Hyg. Méd. soc.*, **11**, 138-143

Loir, A. (1933) *Bull. Acad. Méd. (Paris)*, **109**, 12-14

Loir, A. (1935) *Ann. Hyg. publ. (Paris)*, **13**, 470-475

Ludlam, G. B. (1954) *M.O.H. Monthly Bull.*, **13**, 196-202

Mereshkowsky, S. S. (1895) *Zbl. Bakt.*, **17**, 742-756

Pearson, O. P. (1964) *J. Mammal.*, **45**, 177-188

Pearson, O. P. (1966) *J. anim. Ecol.*, **34**, 217-233

Pearson, O. P. & Baldwin, P. H. (1953) *J. Mammal.*, **34**, 436-447

Pemberton, C. E. (1933) *Hawaii. Plrs' Rec.*, **37**, 12-13

Pimentel, D. (1955) *J. Mammal.*, **36**, 62-68

Schmidt, U. (1954) *Zbl. Bakt., I. Abt. Orig.*, **160**, 487-494

Scient. Amer., 1944, **171**, 81-82

Seaman, G. A. (1952) *Trans. N. Amer. Wildl. Conf.*, **17**, 188-197

Seaman, G. A. & Randall, J. E. (1962) *J. Mammal.*, **43**, 544-546

Spray, R. S. (1926) *J. Amer. med. Ass.*, **86**, 109-111

Swain, R. H. A. (1961) *Vet. Rec.* **73**, 1337-1348

Taylor, J. & Atkinson, J. D. (1955) *Lab. Anim. Bur. coll. Pap.*, **4**, 57-66

Tierärztl Mitt., 1934, **17**, 354

Tomich, P. Q. (1969) *Mammals in Hawaii*, Honolulu, Bishop Museum Special Publication No. 67

Trawiński, A. (1931) *L'extermination du rat à l'aide du système danois en Pologne*, In: *Première Conf. intern. du Rat, Paris, 1928*, pp. 91-95

Uchida, T. A. (1966) *Bull. Wld Hlth Org.*, **35**, 976-980

Uchida, T. A., (1968) *Bull. Wld Hlth Org.*, **39**, 980-986

Uchida, T. A. (1969) *J. Fac. Agric. Kyushu Univ.*, **15**, 311, 354

Walker, R. L. (1966) *Elepaio*, **26**, 96-100

Wodzicki, K., (1950) *Bull. N. Z. Dep. scient. ind. Res.*, No. 98

Wodzicki, K. (1968a) *An ecological survey of rats and other vertebrates of the Tokelau Islands*, Wellington, N.Z. Dep. Sci. Ind. Res., 132 pp.

Wodzicki, K. (1968b) *The Tokelau Rat Survey: 2. Follow-up report*, Wellington, N.Z. Dep. Sci. Ind. Res., 41 pp.

Wodzicki, K. (1969a) *Proc. N. Z. ecol. Soc.*, **16**, 7-12

Wodzicki, K. (1969b) *A preliminary survey of rats and other land vertebrates of Niue Island, South Pacific*, Wellington, N.Z. Dep. Sci. Ind. Res., 41 pp.

Wodzicki, K. (1970) *Report on results of rat control trials in the Tokelau Islands from 30 July to 20 September 1970 and recommendations for a comprehensive scheme of rat control*, Wellington, N.Z. Dep. Sci. Ind. Res., 42 pp.

Zeuner, F. E. (1963) *History of domesticated animals*, London, Hutchinson